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SYMPOSIUM PAPER

Powdery Scab of Potato—Occurrence, Life Cycle and Epidemiology

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Abstract Powdery scab of potato, caused by the zoosporic pathogen *Spongospora subterranea* f.sp. *subterranea* (*Sss*), is an often underestimated disease, which has lead to lack of appropriate control strategies. A new wave of increasing importance of this disease has occurred in the last 30 years in many countries, among them France, Pakistan, Japan, Australia, New Zealand, Costa Rica, USA, and, very recently, Colombia, Korea and China. A consequence is that occurrence of, and research on, powdery scab has shown a cyclic pattern. Additionally to its importance as a pathogen, *Sss* is a vector of potato mop top virus which itself can cause substantial damage. Factors such as intensification of potato production, increasing use of susceptible cultivars, more frequent irrigation and banning of mercury, previously used as an efficient seed tuber treatment, have all contributed to greater incidence of powdery scab. Since 1842, when Wallroth first described the disease in the scientific literature, many researchers, particularly before 1960, started to work with *Sss*, mostly because powdery scab became a problem in their respective countries. Today we know many aspects of the biology of the biotrophic protozoan organism that causes powdery scab, but we still lack basic knowledge on the etiology and epidemiology of the disease. We lack sufficient knowledge of the factors that affect survival of the resting structures, potato and alternative host infection and disease development. This knowledge is essential in predicting disease risk and developing effective powdery scab management strategies.

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Resumen La roña de la papa, causada por el patógeno zoosporico Spongospora subterránea f. sp. subterránea (Sss), es a menudo una enfermedad subestimada, lo cual ha llevado a la falta de estrategias apropiadas de control. Se ha desatado una ola de creciente interés por la enfermedad en los últimos 30 años en muchos países, entre ellos, Francia, Pakistán, Japón. Australia, Nueva Zelanda, Costa Rica, Estados Unidos y más recientemente, Colombia, Corea y China. Una consecuencia es el patrón cíclico en la incidencia de roña y la investigación sobre la enfermedad. Adicionalmente a su importancia como patógeno, el Sss es un vector del virus mop top de la papa, el cual por si mismo puede causar un daño importante. Factores tales como la intensificación de la producción de papa, el creciente uso de cultivares susceptibles, irrigación mas frecuente y la actual prohibición de mercurio previamente usado eficientemente para el tratamiento del tubérculo semilla, han contribuido a la incidencia mayor de roña. Desde 1842, cuando Wallroth describió por primera vez la enfermedad en la literatura científica, muchos investigadores, particularmente antes de 1960, comenzaron a trabajar en Sss, mayormente por que la roña se convirtió en un problema en sus respectivos países. Ahora conocemos muchos aspectos de la biología de este protozoario biotrófico que causa roña, pero todavía carecemos de los conocimientos básicos de la etiología y epidemiología de la enfermedad. No sabemos suficientemente de los factores que afectan la supervivencia de las estructuras de descanso, la infección del huésped alterno y el desarrollo de la enfermedad. Este conocimiento es esencial para predecir el riesgo de la enfermedad y para desarrollar estrategias efectivas para el manejo de la roña.

Keywords Soilborne pathogen · Resting spores · Longevity · Virus vector

Introduction

Powdery scab of potato is caused by the biotrophic protozoan pathogen, *Spongospora subterranea* f.sp. *subterranea* (*Sss*), the only economically significant soil-borne plant pathogen which is also important as a vector of a virus, the potato mop-top furovirus (Kirk 2008). The parasite infects roots, stems and stolons of host plants producing wart-like galls filled with resting spore balls (sporosori). However, the scab-like lesions that are produced on potato tubers and also containing sporosori, are the most damaging as they reduce the proportion of marketable production from crops and carry infection to subsequent crops when the potatoes are used as seed. Powdery scab is an often underestimated disease, especially in the long-term sense, leading to neglect of appropriate control strategies and, sooner or later, to a re-emergence of the disease. A consequence is that the importance of the disease generally shows a cyclic pattern over time in a given country.

In 1842 Wallroth described the symptoms of powdery scab for the first time in the scientific literature in Germany (Wallroth 1842). He concluded that the cause must be a fungus, producing spore balls and called it *Erysibe subterranea*. Later, Brunchhorst (1887) named the pathogen *Spongospora solani*. Lagerheim (1892), having studied the earlier papers, proposed the name *Spongospora subterranea* Wallr. Almost 70 years later, Tomlinson (1958) described a pathogen which caused crook root symptoms on watercress. He found similar sporosori as occurred on potato, and thus proposed two *forma specialis*, *Sss* and *Spongospora subterranea* f.sp. *nasturtii*. In the early 70's Jones and Harrison (1969) proved that *Sss* is the vector of potato mop top furovirus.

Occurrence

History

Powdery scab problems were known by European farmers well before Wallroth presented his paper. He listed several common names which were given to the disease by German farmers. Since then an variety of research projects have been carried out on *Sss*, many of them before 1960. These were often driven by the fact that powdery scab became an increasing problem in national potato production in affected countries. Guessow (1913) received tuber samples from various localities in Canada affected with powdery scab, ".. a disease, well-known in Europe, but as far as I was able to ascertain hitherto not reported as 'established' on any part of the continent of North America.". Only 1 year later, Morse (1914) reported powdery scab for the first time in USA, based on tuber samples received from Nebraska and Massachusetts. He concluded that "…powdery scab is without doubt the most serious disease with which the Maine potato growers have ever had to contend."

In 1916 Melhus et al. published a table on the then current distribution of powdery scab in the United States. This included the states of Maine, New York, Florida, Oregon, Washington and Minnesota. Infected seed tubers which they planted in soils outside Maine did not produce infected crops whereas planting infected seed into the same soils, but this time in Maine, resulted in infected crops. Additionally, healthy seed tubers planted into infested Maine soil, moved to Virginia, produced a mostly infected crop under optimal conditions in a greenhouse experiment. They concluded, that the soil water content, either regulated by precipitation or irrigation, was most important for powdery scab development. Melhus et al. (1916) were the first to describe root galls as symptoms of *Sss* infection.

Apel (1918), a German scientist, published a report on his studies of potato production in the USA. He learned that the USA had stopped import of tubers from all European countries with powdery scab problems, including the UK, Germany and Austria and also Canada. He mentioned the interesting fact that at the time formaldehyde was a common seed disinfectant also used against powdery scab, a chemical which is used nowadays by New Zealand farmers. The differentiation between common scab and powdery scab posed a major problem. Wollenweber (1921) introduced his work with the statement that he started cultivar resistance screening trials and investigated the mode of spread of the powdery scab pathogen because of the increasing importance of the disease in Germany. The Netherlands as an important potato exporter was confronted with serious powdery scab problems in the late 1940s. This situation generated one of the key research projects on powdery scab by Kole (1954).

Current Situation

A new wave of increasing importance or sudden outbreaks of powdery scab has occurred in the last 30 years in many countries, among them Italy (Tuttobene 1986), Turkey (Eraslan and Thurhan 1989), France (Andrivon et al. 2000), Germany (Stachewicz and Enzian 2002), Australia (Hughes 1980), New Zealand (Braithwaite 1994), Pakistan (Ahmad et al. 1996), Colombia (C. Garcia, 2001, personal communication), Japan (Nakayama et al. 2002), Costa Rica (Montera-Astua et al. 2002), and, most recently, Korea (Kim et al. 2003). Today, reports on powdery scab occurrence can be found from almost any of the potato production areas located within the temperate zones of the world (Fig. 1). As demonstrated, the disease has also a long history in North America and, similar to other places, there is again a growing awareness of the importance of the

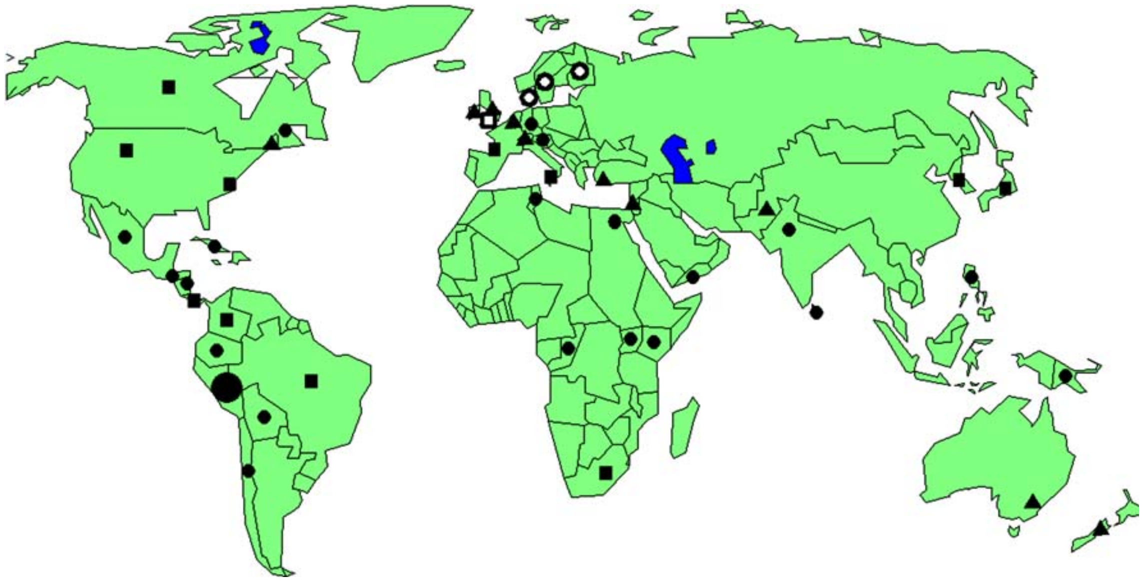

Fig. 1 Countries with a record of *Spongospora*. (●) possible centre of origin of *Sss*; (•) the disease powdery scab has been recorded; (▲) long history of powdery scab research; (■) powdery scab research started more recently; (○) potato mop top virus research (Scandinavia); (◘) centre of *Spongospora subterranea* f.sp. *nasturtii* research (HRI, Wellesbourne, UK)

disease among the potato community in the USA (Christ 2001). New and equally threatening is the recent outbreak of the mop top virus. This was first found in Maine (Lambert et al. 2003) and then in tuber samples from several other important potato producing states of the USA.

In Switzerland potato seed was traditionally produced in the hilly regions of altitude above 600 m, with cool and wet spring climate to prevent virus transmission by aphids. During the second half of the 20th century this production became less economic and seed production shifted towards the lowlands, obviously together with the powdery scab pathogen. In the early 1990s many potato farmers faced serious problems with the new cultivar Agria, which is very susceptible to powdery scab. In 1992 soil samples from about 80 farms were tested for presence of *Sss* using a bait plant bioassay (Merz 1993). The survey showed that many soils in the lowlands of Switzerland were infested with *Sss* (only one fourth was free of infestation), and it was concluded that the disease was much more widespread than previously thought. Interestingly, the same statement was made by Wild (1930) summarizing her findings 60 years previously. This raises the question of whether the pathogen might be endemic and needs a sequence of seasons with optimal conditions to cause disease epidemics.

Currently in many countries factors such as intensification of potato production, increasing use of susceptible cultivars (in Switzerland more than 50% of the potato production is with susceptible cultivars), more frequent use of irrigation, banning of mercury, previously used as an efficient seed tuber treatment, and neglect of prevention measures are all contributing to greater incidence of powdery scab than has occurred previously.

Life Cycle

There are two major phases in the life cycle of *Spongospora*, each initiated by host cell infection through single plasmodia (Fig. 2):

1) The sporangial phase (inner circle of Fig. 2): numerous secondary zoospores are formed in compartments within thin-walled zoosporangia, which develop from multinucleate sporangiogenous plasmodia in the host root epidermal cells or root hairs. The heterocont biflagellate secondary zoospores exit the host and initiate further infection cycles.
2) The sporogenic phase (outer circle of Fig. 2): after nuclear divisions and cleavage within the sporogenic plasmodia, the pathogen produces spore balls (sporosori) each consisting of thickwalled resting spores which are highly persistant. Each resting spore releases a single heterocont biflagellate primary zoospore.

The encircled stages of the life cycle in Fig. 2, and the diploid/haploid status, are still unclear. According to Imgram and Tommerup (1972) and recently supported by Fähling et al. (2004), the life history of the better known member of the Plasmodiophorids, *Plasmodiophora brassicae* Woron., consists of an asexual (represented by the inner circle of Fig. 2) and a sexual phase (outer circle). During the sexual phase, two zoospores fuse and a binucleate/dicaryote plasmodium infects a host cell. The sporogenic plasmodium starts mitotic nuclear division and develops into a large multinucleate plasmodium. Then neighboured nuclei and narrow non-cruciform spindles indicate karyogamy and immediately meiosis occurs prior to resting spore formation.

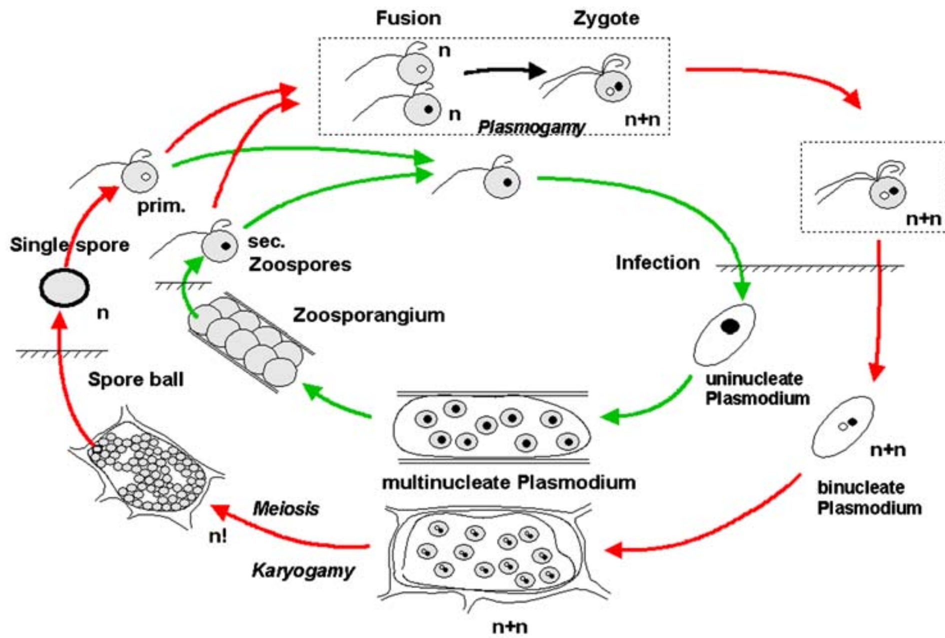

Fig. 2 Tentative life cycle of *Spongospora* species with an asexual phase (*inner circle*) and a sexual phase (*outer circle*)

This remains an assumption, however, until there is unequivocal documentation of karyogamy (Braselton 1995). If a sexual phase also exists in the life cycle of *Sss*, a high degree of genomic diversity should be expected within populations. So far, ITS sequences of field collections originating from different continents have been compared, and only two genetically distinct groups could be identified (Bulman and Marshall 1998; Qu and Christ 2004).

The most important developmental stages in the life cycle of *Sss* have been described (Harrison et al. 1997; Merz 1997). The three-layered walls of the sporosori make them highly resistant to environmental stresses and enable them to survive for more then 10 years in soil. This longevity interferes with our control strategies and explains why prevention of soil contamination is so important. There is no information about the factors that affect the longevity of the resting spores in soil. Further, it is not known whether stimuli are required for zoospore release or if there is a strict dormancy after which resting spores germinate spontaneously and randomly. The primary and secondary zoospores need free water and, once emerged, are able to swim around for about 2 h but need to find host tissue to survive, presumably by means of chemotaxis. Prior to infection, the zoospores encyst, develop an adhesorium and penetrate host cells with the help of an apparatus unique in the Plasmodiophorids, called a 'rohr' and 'stachel'. The first post-infection stage is a uninucleate plasmodium that develops into a multinucleate plasmodium. The stimulus for zoospore release, the chemotactical active root exudates and a favourable environment for encystment, penetration and plasmodial development may all be factors involved with host resistance. The factors that determine whether multinucleate plasmodia form zoospores or resting spores are not known. It is assumed that one zoosporangium originates from a single zoospore. The zoosporangium consists of compartments each containing 4–8 zoospores. When emerging, the secondary zoospores have to squeeze first through an opening in the sporangial wall and then in the host epidermal cell wall.

As the pathogen has the power to produce very large numbers of short and long living propagules in zoosporangia, root galls and tuber lesions, it has very great potential to increase soil infestation within one season.

Damage

The lesions on infected tubers are the most prominent damage caused by *Sss*. For consumers this damage is largely cosmetic as the lesions can easily be removed by hand. Peeling machines are much less successful, and this is the reason why the potato processing industry does have problems with powdery scab. Seed producers can face big financial losses when their seed lots are rejected because of a tuber infection above the generally low tolerance limits. Besides the risk of carrying the pathogen to healthy soils, infected seed can also reduce yield due to the fact that the number of sprouts and the number and weight of tubers per plant are reduced (Falloon 2008). Lesions are weak skin areas with enhanced gas exchange. They allow increased shrinkage and weight loss of stored tubers, or serve as entrance ports for secondary pathogens. Root infection, especially when galls are formed, can cause reduced root function, as indicated by disrupted uptake of water and nutrients (Falloon et al. 2004; Lister et al. 2004).

Epidemiology

The pathogen *Sss* prefers cool and wet climates with optimal temperatures between 12°C and 15°C. Normally, heavy soils with a high clay content or soils with high water capacity encourage the disease, but there are some reports where severe powdery scab has developed in sandy soils. In those places where soil temperature is high or the soil type does not seem to be favourable for infection, irrigation might be the necessary regulation factor (Nachmias and Krikun 1988). Excessive irrigation especially during the period of tuber set as the most susceptible host development stage (Taylor et al. 1986), enables zoospores to swarm and infect susceptible tissue. Today's short crop rotations in intensive potato production do not help to reduce soil inoculum. The role of alternative hosts in the survival of *Sss* may need more attention, particularly in low tillage agriculture. There is no convincing evidence for a direct relationship between soil pH and infection level. It is possible, however, that alteration of pH can change soil characteristics and thus influence infection indirectly.

The resting spores of *Sss* survive in soil for many years. The nature of the longevity is not known but any factor that affects zoospore release also affects the development of powdery scab in the presence of host plants or the reduction of inoculum in the absence of susceptible tissue. The role of rhizosphere microorganisms in the survival of the resting spores remains unclear. Buczacki and Moxham (1983) found that the outermost layers of *P. brassicae* resting spore wall contain mainly protein and that their removal does not diminish spore viability. They interpreted their function as a protecting shell for the inner chitin layer and speculated on the possibility to develop a biocontrol system designed to induce microbial breakdown of spores. It is most likely that the three-layered wall of *Sss* resting spores is composed by the same components. Exudates from antagonistic microorganisms could induce or break spore dormancy, and microorganisms may be involved in the powdery scab suppressive effect of some soils (Harrison et al. 1997).

Little information is available about the relationship between primary inoculum and infection level at harvest. The level of resting spore inoculum in soil required to cause a powdery scab epidemic under given environmental conditions is not known. Also the relative importance of soilborne and seed tuber borne inoculum is not clear. It is also likely that other factors than the inoculum level, such as cultivar susceptibility or weather conditions, are important in development of powdery scab epidemics. If so, there is little hope for the possibility of establishing effective disease risk assessments.

Summary and Outlook

The importance of powdery scab has increased worldwide, due to neglect of the problem on the one hand, and numerous epidemiological factors on the other. It is likely that the infestation level of many soils is close to that which is epidemiologically critical. Potato breeders should focus more attention on powdery scab resistance because many new cultivars are very susceptible to the disease. The pathogen can produce an enormous amount of resting propagules in one season. Resting spores are highly resistant to environmental stress in contrast to the zoospores. Cultivars that produce many root galls need special attention. Powdery scab can cause yield reduction.

We urgently need more data on epidemiologically important factors for the development of integrated powdery scab management based mainly on prevention. Molecular studies on the genetic nature of the Plasmodiophorales in general and *Sss* in particular will reveal details about genomic diversity, the nature of recombination and possibly phylogeography. This background knowledge will be essential for development of more effective powdery scab management.

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